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E-Comment

The Mid-Domain Effect Revisited

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abstract: We revisit the proposition that boundary constraints on species' ranges cause species richness gradients (the mid-domain effect [MDE] hypothesis). In the absence of environmental gradients, species should not retain their observed range sizes as assumed by MDE models. Debate remains regarding the definition of domain limits, valid predictions for testing the models, and their statistical assessment. Empirical support for the MDE is varied but often weak, suggesting that geometric constraints on species' ranges do not provide a general explanation for richness gradients. Criticism of MDE model assumptions does not, however, imply opposition to the use of null models in ecology.

Keywords: diversity, geographic range, geometric constraints, spatial variation, species richness.

As has often been reiterated, many explanations have been proffered for spatial gradients in species richness and most particularly for those associated with latitude. While attention has increasingly come to focus on a small number of these explanations, notably those concerned with variations in area, energy availability, and habitat heterogeneity, debate has continued to revolve around both the plausibility that these are general determinants of observed patterns and the associated empirical evidence (for review, see Gaston 2000; Gaston and Spicer 2004; Ricklefs 2004). The mid-domain effect (MDE), or geometric constraints hypothesis (Colwell and Hurtt 1994; Colwell and Lees 2000), has offered a rather simple, and apparently elegant, additional perspective on richness gradients.

The MDE hypothesis states that the random placement of species' geographic ranges of varying sizes within a region (or domain) bounded by impassable boundaries produces a peak in species richness in the middle of the domain. This so-called MDE has been a general outcome of simulations with theoretical and empirically obtained ranges, as well as of analytical models for both one-dimensional and two-dimensional domains (Colwell and Hurtt 1994; Pineda and Caswell 1998; Willig and Lyons 1998; Lees et al. 1999; Veech 2000; Bokma et al. 2001; Jetz and Rahbek 2001; Grytnes and Vetaas 2002; Laurie and Silander 2002; also see reviews by Colwell and Lees [2000]; Zapata et al. [2003]). On the basis of this result, it has been argued both that the MDE is the most appropriate null model against which to test empirical patterns of species richness along spatial gradients (Colwell and Lees 2000; Jetz and Rahbek 2001) and that domain boundary constraints on species ranges are a contributing cause of species richness gradients (Willig and Lyons 1998; Colwell and Lees 2000).

The MDE hypothesis has stimulated a flurry of empirical and theoretical studies (reviewed by Zapata et al. [2003]; Colwell et al. [2004]; see also Arita 2005) and in a recent review was included among the six most promising hypotheses likely to explain the latitudinal gradient in species richness (Willig et al. 2003). However, several recent contributions have argued that the theory underlying the MDE hypothesis is flawed in the sense that the assumptions are inappropriate rather than that the mathematics is wrong and that the empirical evidence to support the theory is weak (Brown 2001; Koleff and Gaston 2001; Whittaker et al. 2001; Hawkins and Diniz-Filho 2002; Laurie and Silander 2002; Zapata et al. 2003). Colwell, Rahbek, and Gotelli (2004; hereafter CRG) have responded with a long defense of the MDE hypothesis. Unfortunately, this defense fails to address a number of the major criticisms and introduces some additional concerns. Here we briefly summarize these issues.

Null models. CRG confound, at considerable length (in-

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cluding an entire appendix), criticism of MDE models with criticism of null models in general. To our knowledge, at no point have the primary commentators on MDE models sought to argue that the general approach of employing null models is flawed, and indeed many of them have employed null models in other contexts. Likening criticism of MDE models to the debates of the early 1980s regarding the use of null models is to draw a false and rather unhelpful parallel. In the case of MDE models, it is the particulars of the assumptions and tests of these particular models that are being debated, not the philosophy behind or utility of null models. Moreover, arguing that critics of MDE models confuse null hypotheses and null models, and in so doing favor a particular form of statistical assessment of MDE models, perhaps reveals more about the change of perspective on null models by CRG than it does about the view that MDE critics have on null models in general. Gotelli and Graves (1996, p. 3) argue that "the null model formalizes a particular null hypothesis in ecology" and later (p. 7) that "null models rely on the principle of falsification." Gotelli (2001, p. 338) argues that "constructing and testing a null model is straightforward in theory and closely resembles hypothesis testing in conventional statistical analysis." We agree entirely with these statements and are therefore unclear why, for example, CRG (p. E14) argue that MDE models are "null models, but it is shortsighted to treat them strictly as null hypotheses to be rejected or accepted." This change of perspective seems to stem from the claim that the MDE is inevitable (Colwell and Lees 2000) and therefore must always be present to some degree in any species richness gradient.

Geographic ranges. MDE models treat the geographic ranges of individual species as continuous entities. Even accepting this as a convenient first approximation when viewing ranges at a coarse spatial resolution, if MDE models also assume an absence of environmental gradients, then the question is raised as to why all species are not distributed throughout the domain (Hawkins and Diniz-Filho 2002). The only possible mechanism, in the absence of environmental gradients, is dispersal limitation. However, while this is undoubtedly important over very long distances (e.g., between some continents) and is apparently so at regional scales in some instances, there is rather limited evidence that this provides the primary constraint on the continental distributions of the majority of species (Gaston 2003). Environmental conditions have repeatedly been argued to do so (Hoffmann and Blows 1994; Gaston 2003), and such conditions typically show strong spatial gradients. Moreover, the dispersal patterns of species are themselves in part a consequence of environment by genotype interactions (see Zera and Denno 1997; Thomas et al. 2001) that evolve readily. Alternatively, as CRG now seem to argue, MDE models may assume that environmental gradients exist but that species ranges are placed randomly with respect to these gradients. If this is so, then the assumption is also being made that the degree of range cohesion generated by the environment remains constant across an environmental climatic gradient. There is little reason to believe that this is so because the rate of change in environmental conditions and the structure of geographic ranges vary considerably through space (see Gaston 2003).

Domain limits. Colwell and Hurtt (1994) distinguished between hard and soft boundaries to the domains within which species are distributed. They defined hard boundaries as points "beyond which no range may extend" because of physical barriers such as the ocean for terrestrial species or a mountaintop for nonairborne organisms along an elevational gradient. Originally, they also included in this category climatically determined biome limits. In general terms, hard boundaries are physiographical features that impose a barrier to dispersal (Colwell and Lees 2000). Domain limits may also be defined by soft boundaries (Lyons and Willig 1997; Colwell and Lees 2000), which represent a physiological constraint to distribution such as that imposed by temperature tolerance. Critics of MDE theory have identified several difficulties associated with domain boundaries. One concern is the role that hard boundaries actually play in constraining species distributions (Zapata et al. 2003). Although it makes sense intuitively that continental edges should constrain the distribution of terrestrial species (because obviously they cannot occupy marine environments), whether such edges in practice serve directly to determine range limits remains to be demonstrated, given that even those species whose ranges approach coast lines typically reach their limits of distribution well before such edges (presumably for environmental reasons). A similar case can be made for bathymetric and elevational gradients, particularly at great depths and high elevations.

A second concern with domain boundaries is the difficulty of objectively identifying soft boundaries and the circularity in the reasoning behind doing so on the basis of the distribution of a clade (Koleff and Gaston 2001; Zapata et al. 2003). In response, CRG have now compounded this issue by arguing that there should be no distinction between hard and soft boundaries and that all domains should be biologically delimited by the distribution of the clade under study. This reasoning breaks down on closer scrutiny and is also not particularly helpful for understanding patterns in the distribution of diversity. For example, CRG (p. E10) argue that "domain limits for all MDE models are defined biologically by the limits of adaptation of the organisms." Thus, "the concept of the domain of a clade of species rests on the assumption that

the clade collectively displays the evolutionary potential for occupying all points in the domain at some specified period in evolutionary time despite the fact that individual species within the clade are commonly unable to survive and reproduce at every point within the domain." While perhaps stretching the point, given that marine mammals are embedded within the terrestrial mammal groups (as the marine trait is secondarily derived; de Jong 1998; Ursing and Arnason 1998), the domain for a continental group of mammals would under this definition include the sea. Likewise, we suspect that for many terrestrial higher taxa, the notion of hard boundaries disappears under this definition because they do not have species occurring in strictly coastal areas, shifting the emphasis somewhat from geometric constraints and placing it on environmental ones. Clearly, under the logic of CRG, domain boundaries remain rather arbitrary, and MDE models could arguably be criticized for choosing the domain that best fits the data (Pimm and Brown 2004). Certainly, defining domain limits in terms of limits of adaptation runs contrary to a null model approach that allegedly makes minimal biological assumptions because it requires additional considerations regarding the adaptive radiation of tolerances along environmental gradients. The extent to which models that require such levels of external input can be considered null is questionable.

Predictions. CRG (p. E12) argue that "the evidence reveals a substantial signature of MDE in natural patterns." This is based, almost exclusively, on comparison of observed patterns of species richness with those predicted by MDE models. However, this is a relatively weak test of those models, particularly when only some general level of agreement is deemed satisfactory support. As we and others have pointed out, a high coefficient of determination (R^2) could still mean a marked mismatch of species richness values. This point seems to have been missed by CRG (p. E12), who claim that we have assessed studies from an "all or nothing" viewpoint, when in fact we do nothing of the kind (Zapata et al. 2003, pp. 684–688). In this case, the coefficient of determination is a necessary but perhaps not the best guide of the extent to which an MDE model might predict richness, especially because the model output is a set of spatially explicit richness values (albeit this problem is perhaps of less concern when MDE models are being contrasted with other variables in a multiple-variable approach). Assessing the slope and intercept of the relationship between modeled and actual richness provides substantially more information on the extent to which an MDE model predicts observed richness than does a single coefficient of determination (e.g., Jetz and Rahbek 2001).

Presumably, if MDE models had predicted a pattern of richness entirely at odds with that observed, they would never have been proposed as a general explanation for patterns of species richness. Contrary to CRG, strong tests of the models are also provided by examining other predictions that they make. These include spatial patterns of range sizes and spatial turnover in occurrences (for continuous ranges, the latter is essentially the distribution of range endpoints), all of which can be evaluated by quantitative comparisons of model predictions and empirical observations, just as for patterns of species richness. For example, mid-domain models place a set of species ranges, determined from a taxon's range size frequency distribution, at random with regard to a given spatial domain. At each point (or band) within this domain, not only can species richness be calculated, but also two or more adjacent points can be compared with regard to the matching components of diversity, that is, how many species are shared between points, how many species are lost from a focal point relative to its neighbor(s), and how many species are gained by the focal point relative to the others (review in Koleff et al. 2003). Thus, one can calculate null values of these matching components or of beta diversity itself. These can then be compared to the values obtained from the actual species distributions (see Koleff and Gaston 2001). If the models do not predict such patterns, then how well they predict patterns of species richness is irrelevant, as they cannot be capturing the processes determining the patterns of richness. CRG (p. E14) argue that "patterns of turnover do not map 1 : 1 with patterns of species richness because narrow-ranging species differentially affect measures of turnover, whereas wide-ranging species differentially affect spatial patterns of species richness." This, however, is to miss the point. When treating the geographic ranges of individual species as continuous entities, both patterns of species richness and turnover reflect the spatial occurrence of ranges of different sizes, which is precisely what MDE models are predicting.

Tests. CRG (p. E12) argue, based on an evaluation of 21 empirical MDE studies, that "MDE itself is likely to prove an important factor in many patterns of species richness, contrary to the conclusions of authors." Although we remain unconvinced by arguments in favor of using coefficients of determination (without information on slopes and intercepts) for examining MDE models, even using this criterion we are far less sanguine about the outcomes of these tests and the future of MDE models than are CRG. Of the 29 assessments of MDE models that have reported coefficients of determination to date, on a conservative basis (i.e., favoring low R^2 where studies report multiple values), 19 of the assessments report $R^2 \leq 40\%$, and 23 report $R^2 \leq 60\%$ (based on the following studies: Willig and Lyons 1998; Lees et al. 1999; Bokma et al. 2001; Jetz and Rahbek 2001; Kessler 2001; Koleff and Gaston 2001; Diniz-Filho et al. 2002; Ellison 2002; Haw-

kins and Diniz-Filho 2002; Laurie and Silander 2002; Sanders 2002; Kaspari et al. 2003; McCain 2003, 2004; Rangel and Diniz-Filho 2003; Bachman et al. 2004). On an optimistic basis (i.e., favoring high R^2 where studies report multiple values), these figures are 16 and 19, respectively. While in terms of the ecological literature such levels of explained variation are not unreasonable, they belie the fact that CRG dismiss other methods of testing the MDE as inappropriate. This amounts to accepting model fit as evidence of causality, which in isolation is clearly insufficient. By contrast, investigations of hypotheses of other determinants of spatial variation in species richness have generated a large body of tests of model fit but have also tested a wide range of assumptions and secondary predictions of these hypotheses (e.g., Jablonski 1993; Srivastava and Lawton 1998; Bromham and Cardillo 2003; Hawkins and Porter 2003; Currie et al. 2004; Davies et al. 2004; Hurlbert 2004).

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